PRODUCTION AND COLONIZATION OF THE SNAG HABITAT IN A SOUTHEASTERN BLACKWATER RIVER

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PRODUCTION AND COLONIZATION OF THE

SNAG HABITAT IN A SOUTHEASTERN BLACKWATER RIVER

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SUMMARY

Production and colonization of Trichoptera on submerged substrates were studied at two sites on the Satilla River from December, 1974 to November, 1975. The dominant Trichoptera at both sites were members of the family Hydropsychidae: *Hydropsyche orris* and *Macronema carolina* at the lower site and *Hydropsyche incommoda* and *Cheumatopsyche* sp. at the upper site. These animals are all filter-feeders, capturing fine particulate organic matter in their nets.

The natural snag habitat was sampled 18 times throughout the year. Life history information for the major species suggested bivoltine cycles for *H. orris* and *H. incommoda*, and a univoltine cycle for *M. carolina*. Using the Hynes method, the lower site had an annual production for all Trichoptera of about 28 g (dry weight) per m^2 of habitat. Filter-feeders comprised 99.6% of this production, with *H. orris* contributing 78%. The upper site yielded almost 11 g/m^2, with filter-feeders making up 99.9% and *H. incommoda* comprising 95% of this production. These production values are the first that have been reported on Trichoptera inhabiting snags and are the highest for Trichoptera on any type of substrate.

Two kinds of introduced substrate samplers, surface and deep-water, were set out near the lower site in July. Colonization of surface samplers varied considerably over time and never approached the levels of the natural snags. Indigenous wood substrates were more heavily colonized than dowels. Colonization of deep-water samplers approached that of the natural snags after three weeks. Species that were rare after three weeks

appeared in greater abundance after six weeks, causing an increase in diversity but a decrease in total numbers.

Secondary production on the snags is important to the Satilla because little production is associated with the river's unstable sand bottom. Data from natural snags and introduced substrates indicated that secondary production may be limited by habitat availability. Since the snag fauna is an important source of food for fish, the removal of snags as a management practice would probably cause a great decline in invertebrate secondary production as well as fish production.

CHAPTER I

INTRODUCTION

Rivers with shifting sand bottoms and soft, acidic, darkly stained waters are often thought to be unproductive and low in diversity (Hynes 1970, Sioli 1975). The Satilla River, like many coastal plain rivers in the southeastern United States, possesses these characteristics. One might therefore expect these rivers to be impoverished, yet they often appear to have productive fish faunas (Beck 1965, Sandow, Holder and McSwain 1974). Scott (1969) and Gordon and Wallace (1975) observed that fallen trees, brush piles, and rotting limbs are extremely common along the banks of coastal plain rivers and that these submerged substrates can be heavily colonized by invertebrates. Scott (1969) suggested that filter-feeding organisms were the major colonists on these natural substrates, or snag habitat, and were the most important energy processors in the river. The objectives of the present study were: (1) to estimate secondary production of the Trichoptera, the major filter-feeding group on the snag habitat, and (2) determine their rate and pattern of colonization.

Previous work has shown that most lotic systems receive the majority of their organic input from allochthonous sources (Nelson and Scott 1962, Hynes 1970, Cummins, Peterson, Howard, Wuycheck, and Holt 1973). An important component of such systems is the filter-feeders, to which group many of the Trichoptera belong (Cummins 1973, 1974). In particular, the family Hydropsychidae is often found in large numbers in riverine systems throughout the world (Hynes 1970). In the Satilla, this group dominated the community inhabiting the snag habitat.

Several estimates of secondary production in lotic systems have been made in recent years (Mann 1975), but no estimates are available for snag habitats. Those few works which have been conducted where there existed habitats similar to the snags in the Satilla have not attempted to estimate secondary production (Nilsen and Larimore 1973, Nord and Schmulbach 1973).

In addition to sampling the natural snag habitat, some knowledge of colonization was needed in the present study because there were considerable fluctuations in water level and submerged available habitat. Colonization of introduced substrates provided information on how fast newly inundated substrates could be colonized. Furthermore, since natural snag samples could only be collected near the water surface, it was important to learn if snag colonization near the bottom was similar to that at the surface.

CHAPTER II

STUDY AREA

The Satilla River flows entirely through the Coastal Plain of Georgia for 362 km before emptying into the Atlantic Ocean at St. Andrew's Sound near Brunswick, Georgia (Fig. 1). Organic materials washed out of adjacent cypress-gum swamps, which are flooded throughout much of the winter and early spring, give the river its characteristic "blackwater" designation. The State of Georgia (Environmental Protection Division, 1975) monitors water quality several times a year on the Satilla. Also, Beck, Reuter and Perdue (1974) conducted a detailed analysis of both inorganic and organic constituents. Water quality on the river is considered good to excellent with the following general characteristics: (1) a pH ranging from 4.3 to 6.8 with a mean of 5.0, (2) a low turbidity averaging 6.3 JCU, (3) highly colored water, with an average of 159 Pt-Co units, (4) a low ionic strength with specific conductance averaging 45 μmho cm^{-1}, and (5) a predominance of organic over inorganic constituents. The water temperature ranges from 5.5^{o} to 26.0^{o}C, with temperatures above 20^{o}C from May through October.

Two sites on the Satilla were chosen for sampling: an upper one about 13 river kilometers north of Waycross, the other about 16 river kilometers below the Highway 84 bridge near Atkinson (Fig. 1). The lower site was approximately 129 river kilometers from the coast with the upper site another 161 km further upstream. Both study sites lie in the topographic region known as the Coastal Terraces, covered by Pleistocene sands

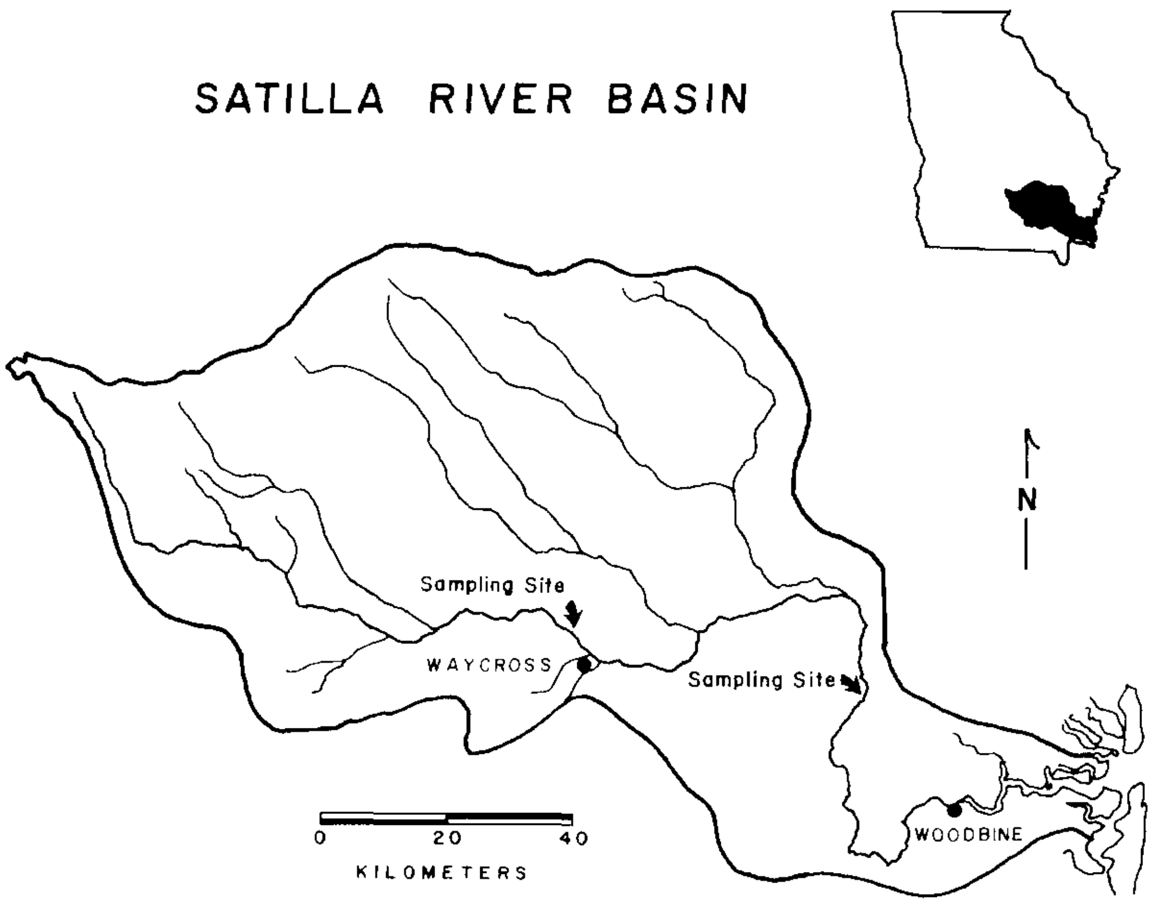

Fig. 1 Satilla River Drainage Basin with Location of Upper and Lower Sampling Sites.

and sandy loams, except in swamps where the sands are overlain by muck or peat (LaForge, Cooke, Keith, and Campbell 1925).

Discharge from December 1974 through November 1975 ranged from 6.9 to 504 m^3/sec at the lower site and 2.9 to 280 m^3/sec at the upper site (Fig. 2). Even lower values were seen in the autumn prior to sampling and in the spring following sampling. Current velocity in the channel varied from 0.214 to 0.916 m/sec at the lower site and from 0.228 to 0.686 m/sec at the upper site.

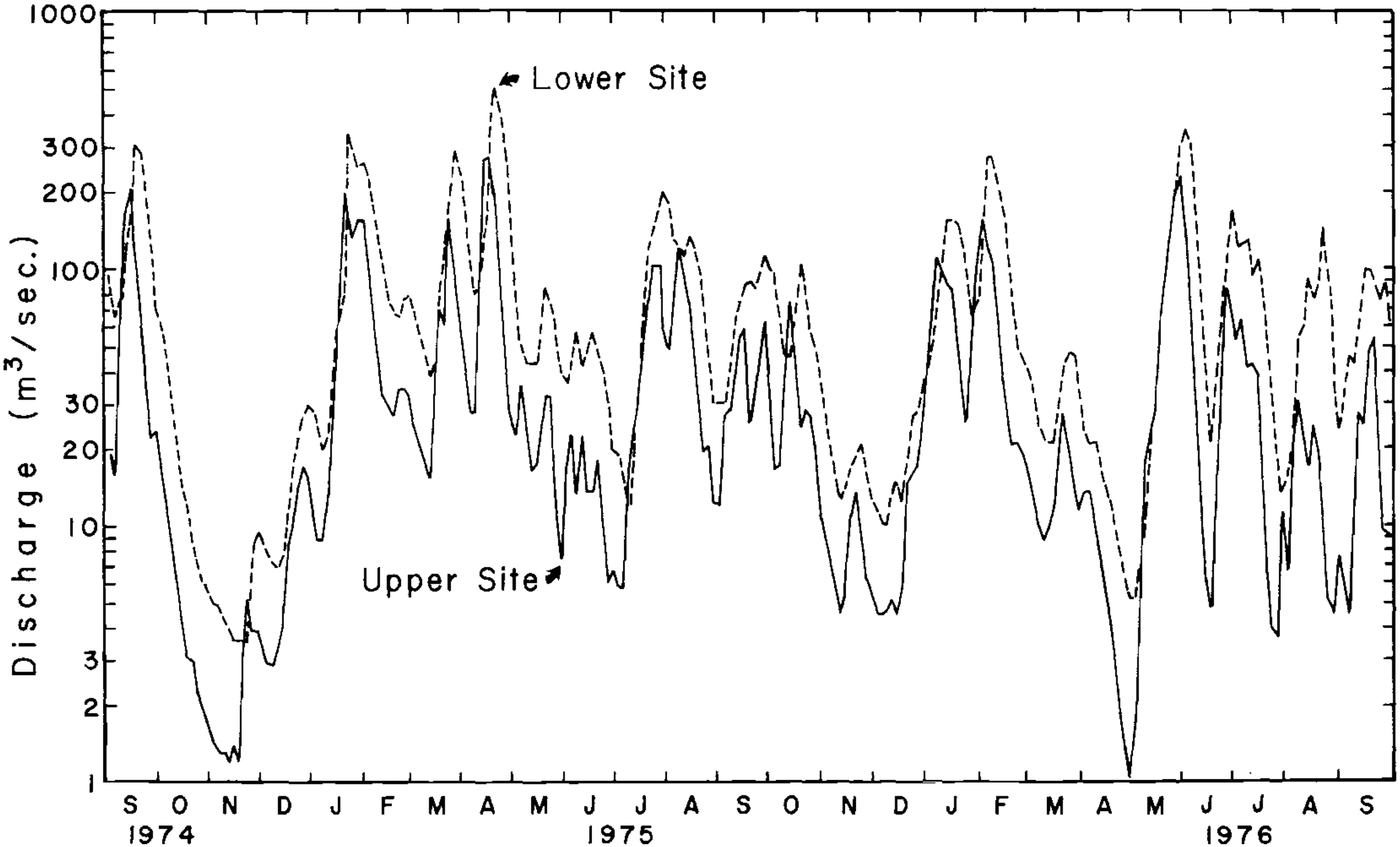

Fig. 2. Discharge of the Satilla River at Upper (Waycross) and Lower (Highway 84) Sampling Sites.

CHAPTER III

MATERIALS AND METHODS

Monthly samples of six snags were taken at each site from December, 1974 through November, 1975, with semimonthly samples collected from May through August. These were taken from a boat in the channel, usually in the top meter of the water column along the bank. A net was placed under and behind a section of the snag. The snag was cut, and quickly transferred to a bucket. Relatively few animals ever dropped into the net and thus few were believed to have been lost during this procedure. The sample was then preserved in dilute formalin until further processing.

Once in the laboratory, the contents were placed in a white porcelain pan and washed with running water. A 0.10 mm sieve was used to remove excess water. The remaining animals were then removed by careful examination under a magnifying light. The animals thus obtained were placed into jars containing 80% ethanol.

Habitat surface area was calculated by measuring the length and mean diameter of each segment of snag. Animal densities and standing stocks could then be calculated for a square meter of habitat surface. The animals were separated from the detritus, identified, and head widths were measured using an ocular micrometer accurate to 0.01 mm. Dry weights for the common species were obtained by placing fresh specimens in an oven set at 60°C for 24 hours. Instar weights were usually estimated by log-log regressions of head width (or length) and dry weight.

The Hynes and Coleman (1968) method, modified by Hamilton (1969), was used here to directly estimate production. This method was originally introduced to allow production estimates to be made of entire faunal assemblages or asynchronously developing populations. In this study, it was used on an individual basis for the major species. The less numerous species were grouped into families for production calculations. The most accurate estimates would be expected when the method is applied to single species. To calculate production, the average size-frequency distribution was calculated from samples collected throughout the year. This size distribution was assumed to approximate the survivorship of an average cohort and it was assumed that the number of cohorts equaled the number of size classes.

The Hynes method originally used volumetric units. Here weight was substituted for volume, giving the following:

$$P_w = i \sum_{j=1}^{i} (\bar{n}_j - \bar{n}_{j+1}) \left(\frac{W_j + W_{j+1}}{2}\right), \text{ where}$$

P_w = estimated annual production in weight units,

$\bar{n}_j$ = mean number of individuals in weight class j,

W_j = median weight of weight class j,

i = number of weight classes or instars that a population grows through to reach its maximum weight,

$\bar{n}_{i+1}$ = zero, since length class i is the last length class containing organisms.

$W_{i+1} = W_i$, since the weight value for the final term in the summation must equal the final instar weight

It was assumed that: (1) the species were univoltine, (2) individuals all grew to the maximum weight, and (3) they remained in each of the size classes for the same amount of time. If the species was not univoltine, the calculated production value must be multiplied by the number of generations per year.

Fager (1969) and Zwick (1975) criticized the Hynes method as being sensitive to non-linear growth, but both misinterpreted the concept of the average cohort. Hamilton (1969) and Benke and Waide (1977) have shown that non-linear growth had little effect on the final production estimate. Hamilton showed how to correct for non-linear growth if the length of time spend in each size class is known.

To obtain more information on colonization, two types of artificial samplers using indigenous wood were set out at the lower site in July, 1975. The first type consisted of two surface samplers that contained 25 "snags", five in each of five rows (Fig. 3). The branches extended roughly 25 cm into the water and ranged from .01-.03 m^2. Float A contained firm wood only, while Float B had three types of wood: firm, partially decomposing, and dowel, to test for colonization preferences of wood type. All wood (except dowels) was taken from trees along the river. The styrofoam floats were secured with rope to overhanging limbs and placed in the channel approximately 20 m apart. Sampling consisted of removing a particular row or rows (which were oriented parallel to the current), and replacing them with branches of known surface area.

Two deep-water samplers were also distributed at each of two locations, with an individual sampler containing four parallel pieces of wood

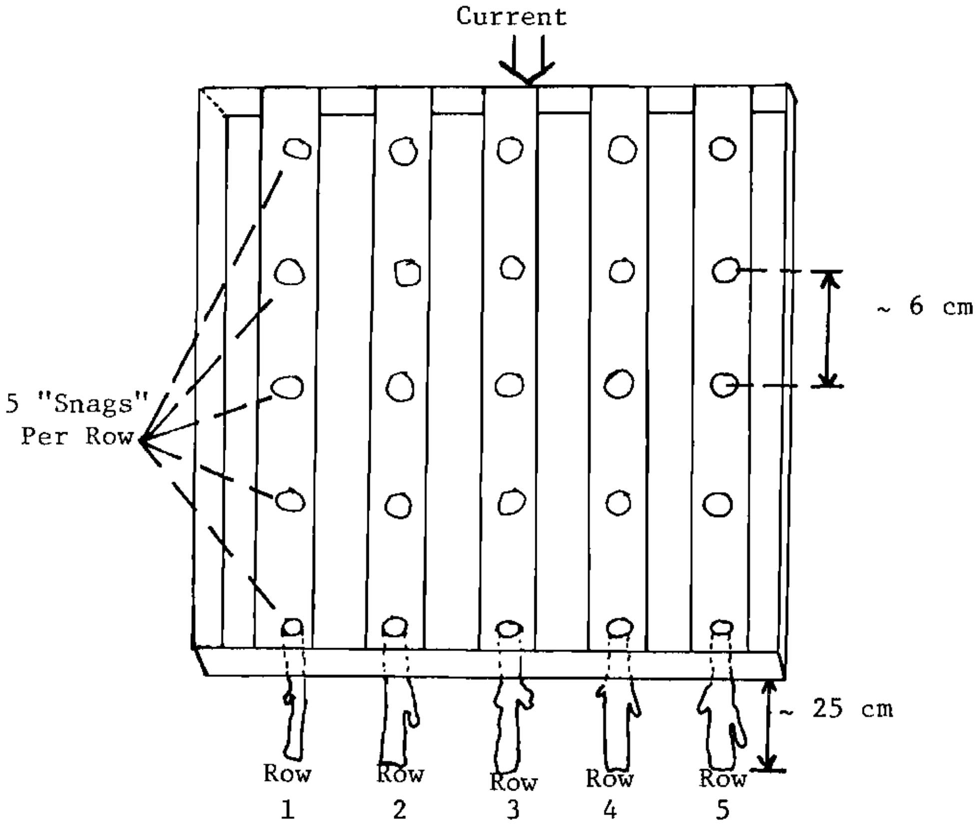

Figure 3. Surface Sampler

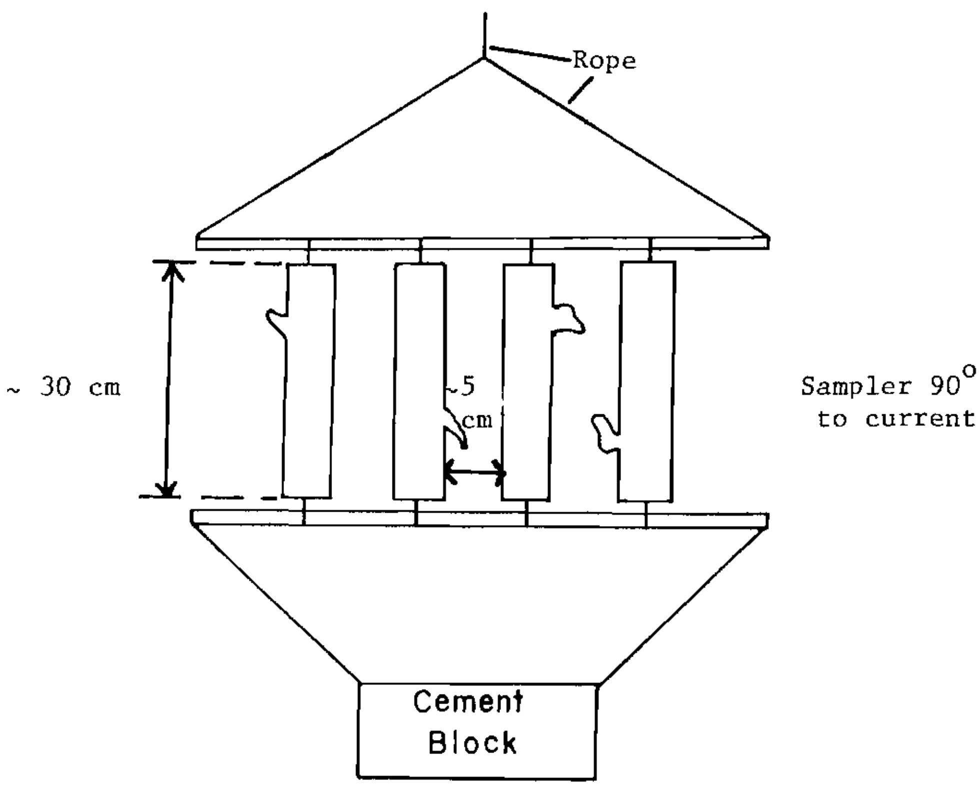

Figure 4. Deep-water Sampler

oriented perpendicular to the current (Fig. 4). Samplers 1 and 3 were placed at one location, Samplers 2 and 4 at another; both locations were near the lower river study site. The samplers were about 1.5-2.0 m deep and the branches ranged from .023-.045 m^2. One sampler was removed from each location after three weeks and the remaining samplers were collected after six weeks.

The artificial samplers were processed in the same manner as was described for the natural snags. One exception involved the deep-water samplers, which had to be carefully pulled toward the surface until a net could be placed under a particular branch. This was done before allowing the sample to break the water surface, in order to reduce loss of animals.

CHAPTER IV

RESULTS

Species Composition

Hydropsyche orris, *Macronema carolina*, and *Chimarra* sp. were the most abundant trichopterans on the lower site snags (Table 1). Seven other caddisflies were found in lesser numbers. A few members of the Hydroptilidae were also taken, but were not included here due to their very low numbers.

At the upper site, *Hydropsyche incommoda* and *Cheumatopsyche* sp. were the most abundant, while *Chimarra* sp. was still common (Table 1). All the organisms present at the lower site were found to some degree at the upper site. The major difference in species composition at the two sites was a change in the dominant organisms, all belonging to the family Hydropsychidae. Hydropsychids are all filter feeders, capturing fine particulate organic matter present in the flowing water.

Instars and Life Histories

Determination of size classes was necessary to follow life histories and obtain production estimates. Most of the trichopterans found in the Satilla displayed distinct instars (Fig. 5). Head width (except for *Chimarra* sp., which was head length) frequency histograms indicated that *H. orris*, *M. carolina*, *Chimarra* sp., and *H. incommoda* had five instars. *Cheumatopsyche* sp., *Neureclipsis* sp. and *Cyrnellus* sp. had four identifi-

Table 1. Trichoptera present on snags at two sites on the Satilla River. (***abundant, **common, and *rare, based upon densities and frequencies).

Organism	Lower Site	Upper Site
Hydropsychidae		
Cheumatopsyche sp.[1]	*	***
Hydropsyche incommoda Hagen	**	***
Hydropsyche orris Ross	***	*
Macronema carolina Banks	***	**
Leptoceridae		
Ceraclea sp.	**	**
Oecetis spp.	**	*
Triaenodes sp.	*	*
Philopotamidae		
Chimarra sp.[2]	**	**
Psychomyiidae		
Cyrnellus sp.	**	**
Neureclipsis sp.	**	**

[1] probably *C. pinaca* Ross or *C. pasella* Ross based upon their distribution in Savannah River Basin, Gordon and Wallace (1975).

[2] probably *C. socia* Hagen (J.B. Wallace pers. comm.)

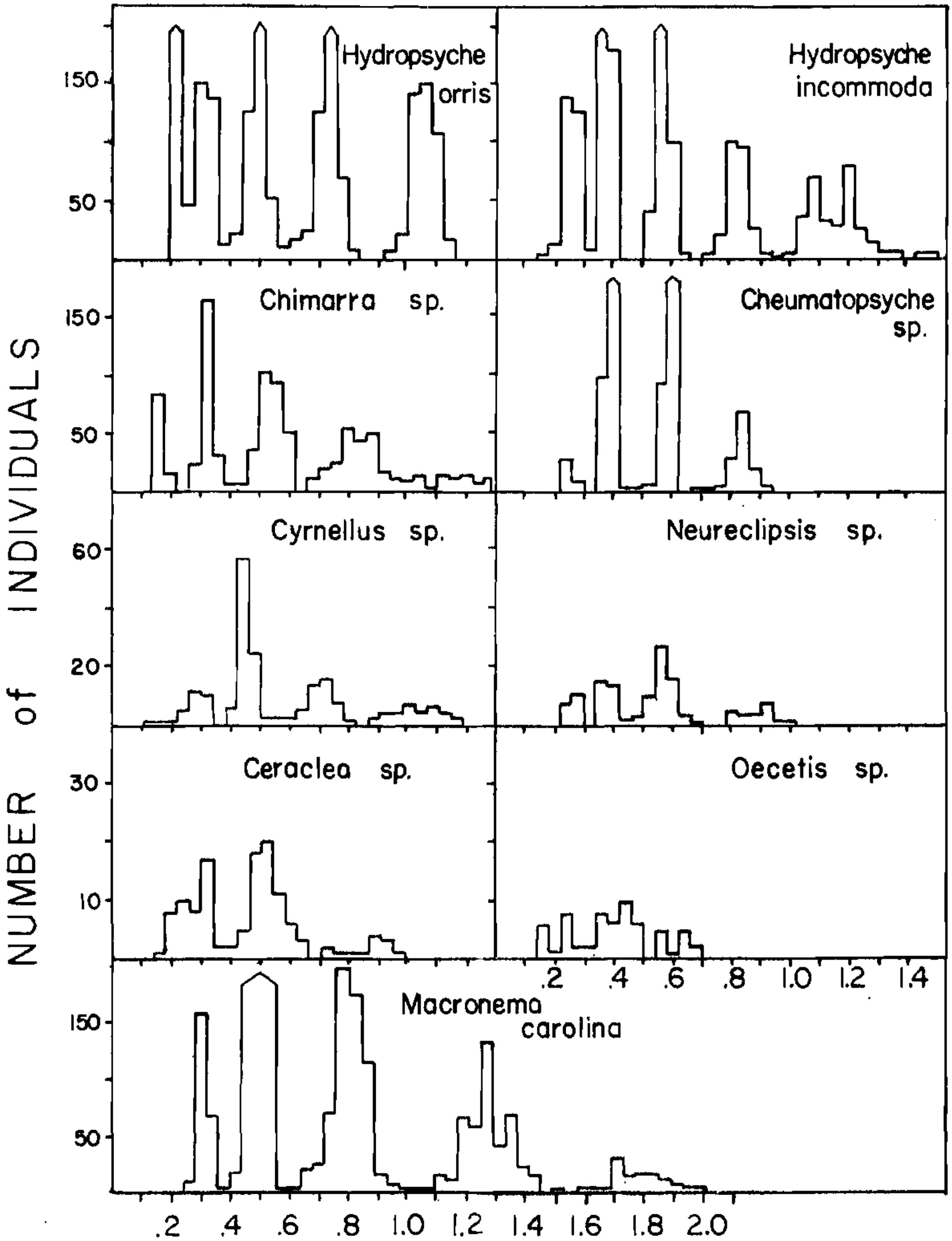

Figure 5. Head Width (Length for Chimarra sp.) Frequency Histograms for Trichoptera in the Satilla River

able instars. Instars of the other three caddisflies (Leptoceridae) were difficult to determine due to their low numbers and morphological similarities.

Instar frequency histograms for each sampling date provided life history information of the dominant species (Fig. 6). H. orris appeared to be bivoltine with the highest recruitment occurring in May - June and September. However, since no sample was taken between 30 August and 3 October, the later recruitment peak with first instars was not observed. The occurrence of pupae in May and August preceded these recruitment periods. The presence of early instars from May through 19 July, and low numbers of pupae during this same period indicated an extended reproductive period for the first generation.

The size-frequency histograms indicated the presence of one generation per year for M. carolina. Pupae appeared in May and recruitment was highest from late May through early June. The presence of first instar larvae throughout the summer and fall again indicates an extended recruitment period.

H. incommoda displayed two generations per year with a long recruitment period in May - July and a shorter one in September, similar to H. orris. Pupae occurred mostly in late May to early July and again from late August to early October.

The remainder of the Trichoptera did not provide enough information to obtain adequate life histories. Chimarra sp. had a fairly even size distribution throughout the year. For it and the other species, the conservative assumption of one generation per year was made.

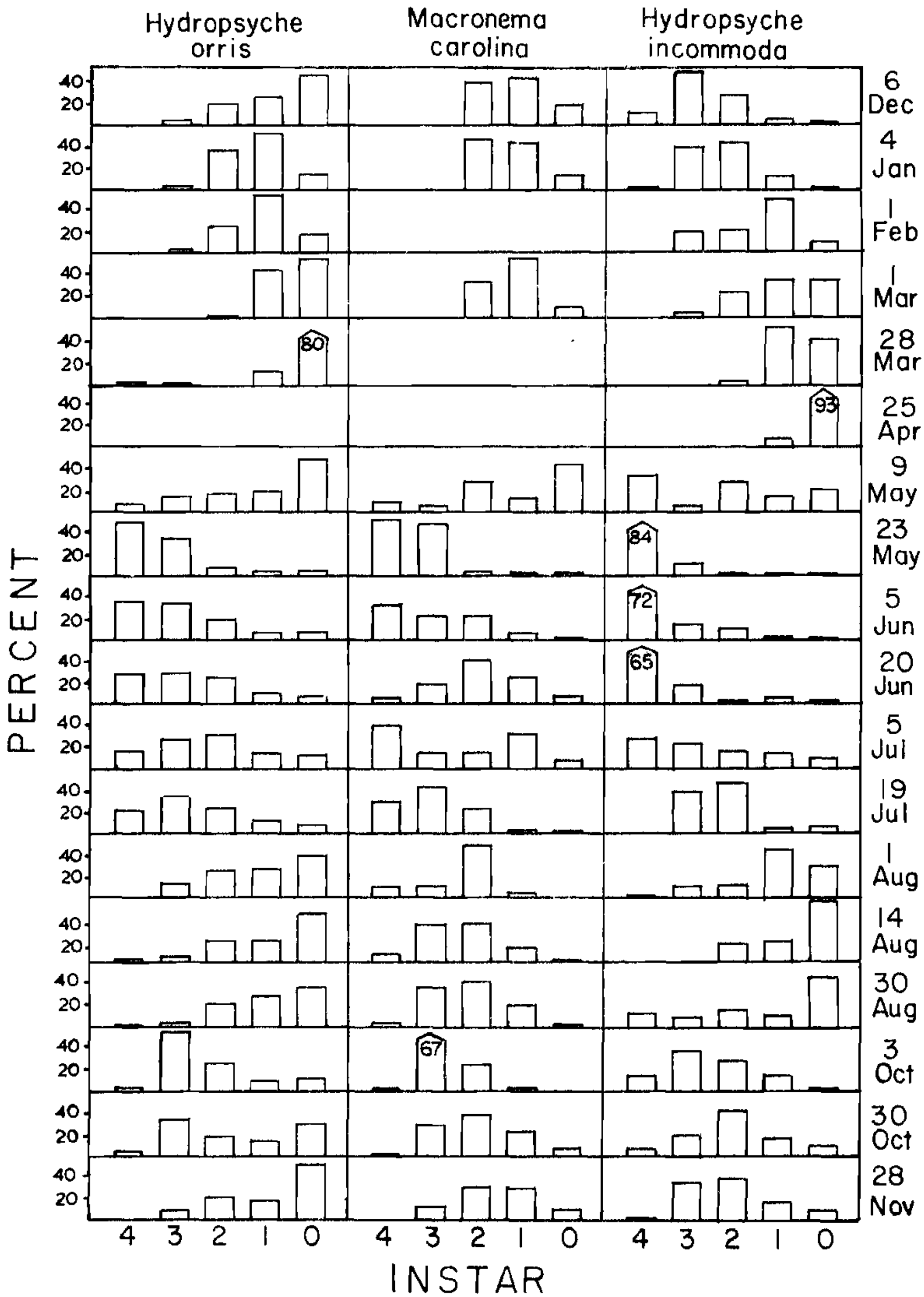

Figure 6. Instar-frequency Distributions for the Dominant Trichoptera from Dec. 1974 through Nov. 1975 (Final Instar = 0, Penultimate = 1, Antepenultimate = 2, etc).

Instar Biomass

Biomasses were determined for most species by log-log regressions as mentioned previously. Table 2 gives the values for the major species. For *H. orris*, actual means of each instar were used instead of a regression due to a very large sample size at each instar. At the time dry weights were taken, *Cheumatopsyche* sp. was not available. Values of comparable sizes of *H. incommoda* (except shifted down one instar) were substituted for *Cheumatopsyche* sp. In general, the table shows that for the Hydropsychidae, biomass roughly triples with each instar.

Densities and Standing Stocks

At the lower site, *H. orris* had a standing stock ranging from 0.8 g/m^2 of snag surface in February to 14.2 g/m^2 on 5 July, while density varied from 305 to 41.997 animals/m^2 on the same respective dates (Fig. 7). The ranges given here from the lower site exclude 25 April when no trichopterans were found due to flood conditions. Other values are probably attributable to rapidly rising water levels (Fig. 2), with little colonization of recently inundated snags near the surface). *M. carolina* was the second most abundant caddisfly on the lower site snags. Standing stock ranged from virtually nothing during rising waters to 2.9 g/m^2; density varied from one to 10,037 animals/m^2 (Fig. 7). In general, the greatest standing stocks and densities were found on four consecutive sampling dates from 23 May to 4 July. *Chimarra* sp. density and standing stock ranged from 6 to 2370 animals/m^2 and 0.0 to 0.3 g/m^2, respectively (Fig. 7). The other trichopterans combined had their

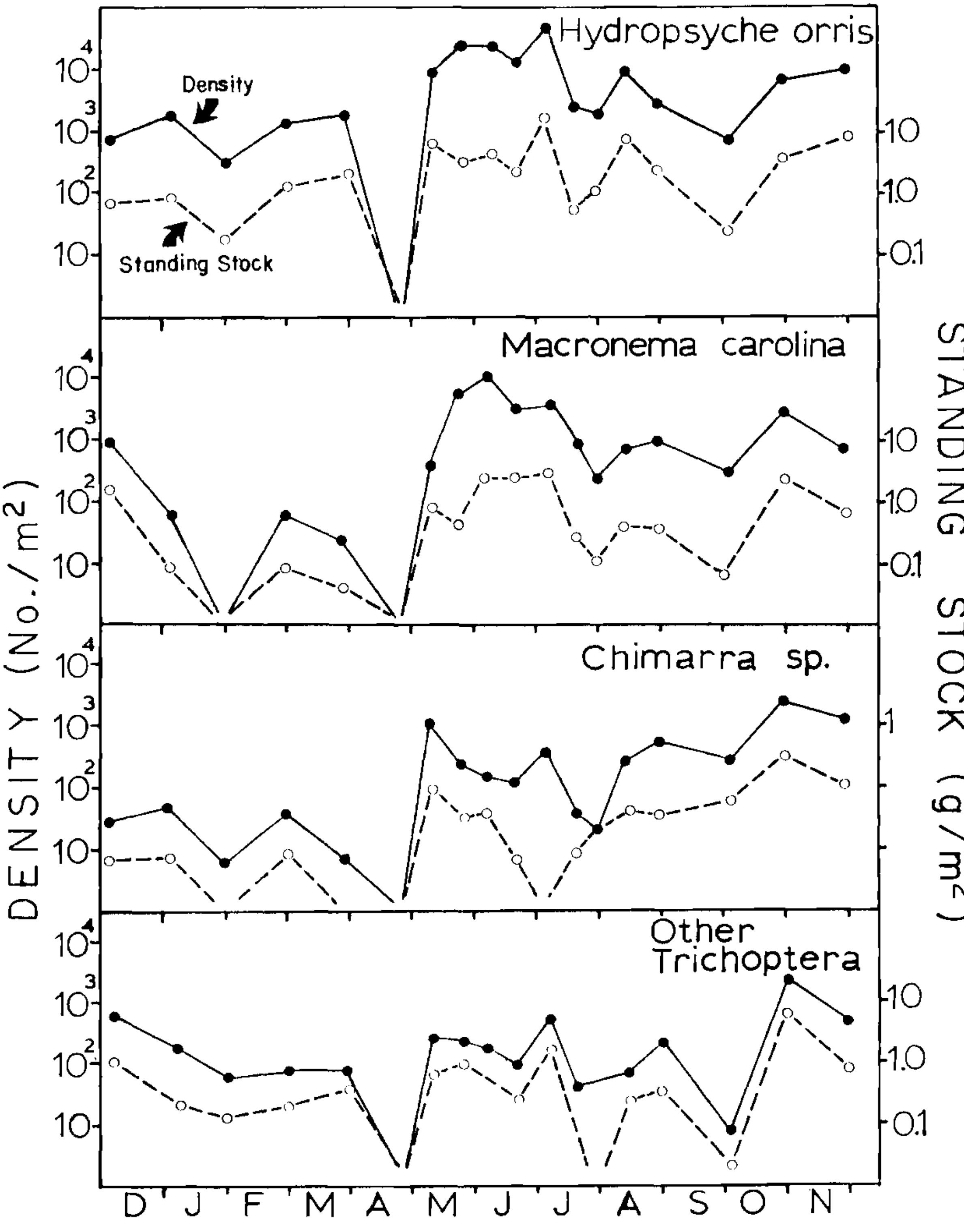

Figure 7. Mean Density and Standing Stock for the Dominant Trichoptera from Dec. 1974 through Nov. 1975, Lower Site.

Table 2. Mean dry wt.(mg) for instars of the more common Trichoptera

Species	Instar F-4	F-3	F-2	F-1	F
Cheumatopsyche sp.		.02	.07	.21	.74
Chimarra sp.	.00	.01	.04	.21	.50
Hydropsyche incommoda	.02	.07	.21	.62	1.71
Hydropsyche orris	.02	.06	.15	.42	1.50
Macronema carolina	.03	.11	.37	1.43	3.81

greatest values in late fall-early winter, with densities reaching 2473 animals/m^2 on 30 October and standing stocks obtaining a maximum value of 0.7 g/m^2 on the same date, mainly due to a large number of *H. incommoda*. Overall, the greatest numbers of caddisflies were in late spring-early summer, while high standing stocks occurred at various times from spring until late fall.

While densities and standing stocks at the upper site did not attain the magnitude of those figures at the lower site, the maximum values were still fairly high (Fig. 8). *H. incommoda* had its highest value for density, 16,474 animals/m^2, occurring surprisingly in December. Standing stock reached 5.8 g/m^2 on 30 August. *Cheumatopsyche* sp. exhibited its greatest values, 2,767 animals/m^2 and 0.6 g/m^2, on 4 January. As was the case at the lower site, the other trichopterans combined had their maximum values from late summer to early winter.

Production, Turnover Ratios and Mean Annual Standing Stocks

Production calculations for the dominant species are presented in Table 3 for the lower site and Table 4 for the upper site. It was assumed that the snag animals lost to drift were replaced simultaneously, maintaining a constant population.

At the lower site, summing the losses between instars gave a value of 11.1 g/m^2 for *H. orris*. This must be multiplied by two (generations per year), which yielded an annual production of 22.1 g/m^2 of habitat. The mean annual standing stock was 3.4 g/m^2, giving an annual turnover ratio (TR) of 6.4. Negative values for losses of *H. orris* (Table 3)

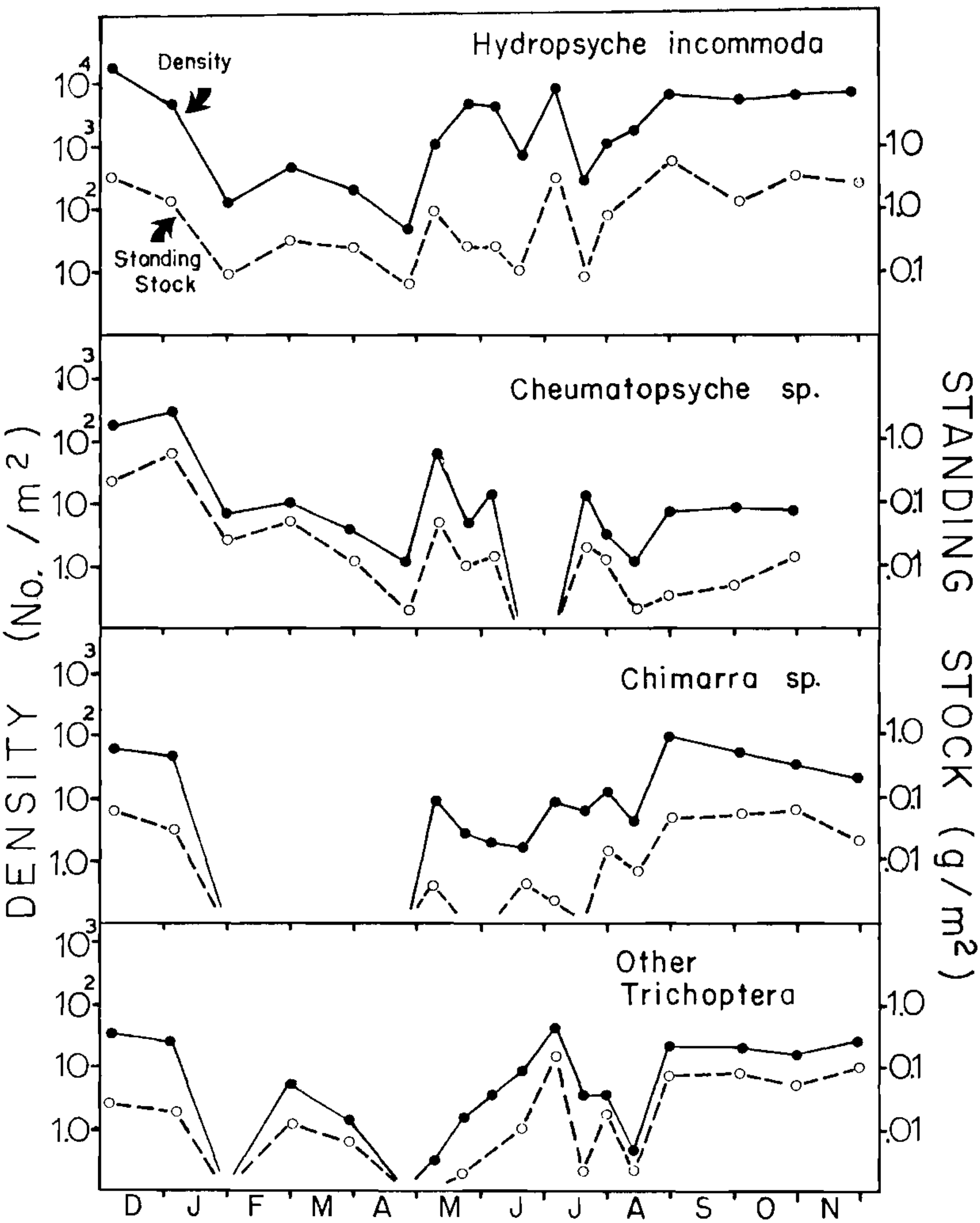

Figure 8. Mean Density and Standing Stock for the Dominant Trichoptera from Dec. 1974 through Nov. 1975, Upper Site

Table 3. Production of dominant Trichoptera at the lower site, using the Hynes method.

Size Group	No./m^2	Mean wt.(mg)	Standing Stock(g/m^2)	No. lost / m^2	Wt. at loss(mg)	Wt. loss (g/m^2)	X 5 (g/m^2)
			Hydropsyche orris				
F-4	1927.7	0.02	.04				
				-114.4	.04	-.01	-.05
F-3	2042.1	0.06	.12				
				296.9	.11	.03	.18
F-2	1745.2	.15	.26				
				606.2	.29	.18	.90
F-1	1139.0	.42	.48				
				-557.1	.96	-.53	-2.65
F	1696.1	1.50	2.55				
				1696.1	1.50	2.54	12.72
							11.10
Mean Standing Stock =			3.45			X 2 gen./yr. =	22.20
			Macronema carolina				
F-4	497.9	.03	.02				
				0.2	.07	-	
F-3	497.7	.11	.06				
				103.6	.24	.03	.15
F-2	394.1	.37	.15				
				156.5	.90	.14	.70
F-1	237.6	1.43	.34				
				133.6	2.62	.35	1.75
F	104.0	3.81	.40				
				104.0	3.81	.40	2.00
Mean Standing Stock =			.97				4.60
			Chimarra sp.				
F-4	42.6	.00	.00				
				-60.3	.00	.00	.00
F-3	102.9	.01	.00				
				-16.6	.02	.00	.00
F-2	119.5	.04	.01				
				26.4	.13	.00	.00
F-1	93.1	.21	.02				
				56.2	.36	.02	.10
F	36.9	.50	.02				
				36.9	.50	.02	.10
Mean Standing Stock =			.05				.20

Table 4. Production of dominant Trichoptera at the upper site, using the Hynes method.

Instar	No/m²	Mean wt. (mg)	Standing Stock (g/m²)	No. lost / m²	Wt. at loss (mg)	Wt. loss (g/m²)	X 5 (g/m²)
			Hydropsyche incommoda				
F-4	881.2	.02	.02				
				-306.2	.05	-.01	-.05
F-3	1187.4	.07	.08				
				208.7	.14	.03	.15
F-2	978.7	.21	.21				
				481.0	.43	.20	1.00
F-1	497.7	.62	.31				
				25.7	1.17	.03	.15
F	472.0	1.71	.81				
				472.0	1.17	.81	4.04
							5.29
Mean Standing Stock =			1.42			X 2 gen./yr. =	10.58
			Cheumatopsyche sp.				
F-3	11.0	.02	.00				
				-172.8	.05	-.01	-.05
F-2	183.8	.07	.01				
				75.8	.14	.01	.05
F-1	108.0	.21	.02				
				66.0	.48	.03	.15
F	42.0	.74	.03				
				42.0	.74	.03	.15
Mean Standing Stock =			.06				.30

could be due to a decreased efficiency in collecting the smallest individuals, or because the larvae may spend a greater part of their life cycle in the final instar relative to other instars. The latter negative value can be corrected if the length of time spent in each instar is known (Hamilton 1969). However, without such knowledge, it is important to retain negative values in the table.

Table 3 also presents the production calculations for M. carolina and Chimarra sp. Production for the former was based on one generation per year, which the size-frequency histograms and pupae indicated. Chimarra sp. is presented in tabular form, despite the fact that H. incommoda was more productive at the lower site, because it was a common species at both study sites.

A summary of values for the caddisflies is presented in Table 5. The members of the Psychomyiidae and Leptoceridae together contributed little to the total annual production. Total trichopteran production at the lower site was 27.5 g/m^2. Of these totals, H. orris contributed 78% to production and 76% to the standing stock.

At the upper site, H. incommoda was the most productive, yielding annually 10.6 g/m^2 of habitat, with a mean annual standing stock of 1.4 g/m^2 (Table 4). This resulted in an annual TR of 7.4. Production then fell sharply for the other species, Cheumatopsyche sp. being the next most productive. Of the remaining species (Table 5), Chimarra sp. had an annual production of about half of that found at the lower site. The Leptoceridae and Psychomyiidae were again grouped at the upper site, giving a combined value of .05 g/m^2. H. orris and M. carolina together

Table 5. Annual production and turnover ratios of Trichoptera at two sites on the Satilla River.

	Lower Site		Upper Site	
	Annual Production (g/m^2)	Annual Turnover Ratio	Annual Production (g/m^2)	Annual Turnover Ratio
Hydropsyche orris	22.14	6.4	.15**	
Macronema carolina	4.56	4.7		
Chimarra sp.*	.21	4.9	.10	5.3
Hydropsyche incommoda	.45	9.0	10.57	7.4
Cheumatopsyche sp.*			.26	3.9
Leptoceridae*	.11	4.8	.02	5.0
Psychomyiidae*	.06	4.3	.04	5.8
Total	27.53		11.14	

* Generation time unknown; assumed to be univoltine.

** Includes *M. carolina*; no TR because two species had different number of generations per year.

contributed 0.2 g/m^2 annually.

Total production at the upper site was 11.1 g/m^2. The total mean annual standing stock was 1.6 g/m^2. Of these totals, *H. incommoda* comprised 95 and 91%, respectively.

Colonization of Artificial Samplers

From 14 July - 3 September, Row 1 of surface sampler Float A was sampled and replaced with new snags five times at ten day intervals (Fig. 3). These samples provided an indication of colonization rates for short intervals over a 50 day period. After these ten day intervals, *H. orris* and *M. carolina* were the only caddisflies to have substantially colonized the branches (Fig. 9a, b, c). The colonization of both species showed a significant difference ($P < .01$) between dates over the 50 day period. Colonization decreased as August progressed. During this period, recruitment was not occurring for either species. However, the river discharge dropped from 200 m^3/sec on 1 August to 28 m^3/sec on 3 September (Fig. 2). It is possible that the drop in current the last half of August accounted for some of the variability in colonization rates.

Rows 2, 3, 4 and 5 of Float A were sampled at 20, 30, 40 and 50 day intervals, respectively. These samples indicated colonization rates for cumulative intervals over a 50 day period (Figs. 9d, e, f). No significant difference between means ($P > .05$) was found when testing combined trichopteran densities between intervals. To illustrate this further, the 50 day colonization figures on 3 September were less than those for the 20 day interval on 3 August for both *H. orris* and *M. carolina*. The

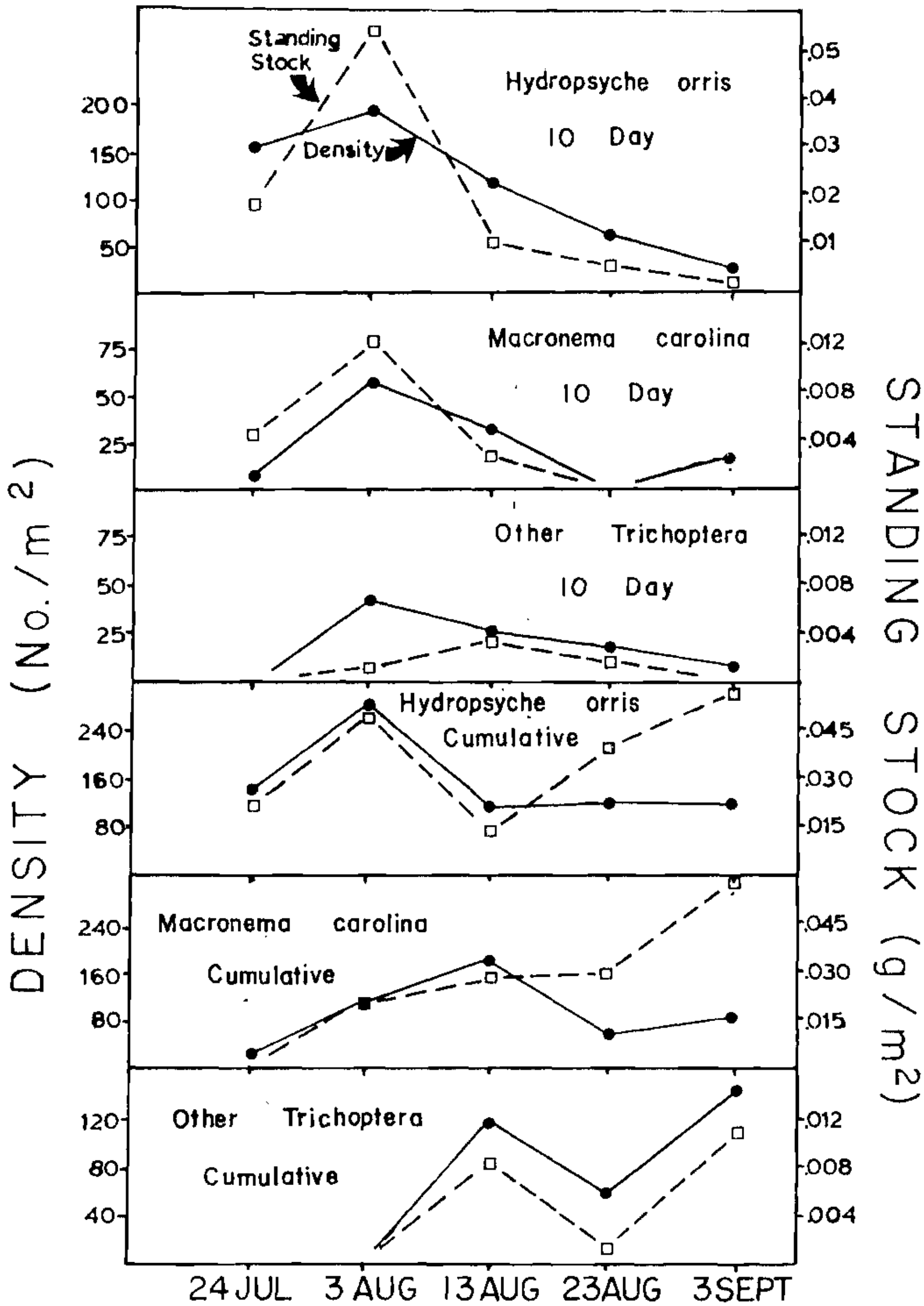

Figure 9. Colonization of Snags on Float A (a, b, c - 10 Day Colonization Period; d, e, f - Cumulative Colonization for 10, 20, 30, 40 and 50 Day Intervals).

cumulative densities and standing stocks never went much above what could be achieved on a ten day interval. Although the figures varied, they never fell below 301 animals/m^2 or 0.06 g/m^2 (for all trichopterans). There was some indication that other species, particularly *Chimarra* sp., required a longer period of time to colonize. The totals for the 50 day colonization, 470 animals/m^2 and .13 g/m^2, did not approach the values of the natural snags, which were 4816 animals/m^2 and 3.3 g/m^2 on 30 August.

Surface sampler Float B tested for wood-type colonization preferences (Table 6). For the hydropsychids, no significant difference was found for colonization of firm versus partly decomposing wood for either 20 or 50 day intervals. A t-test between means showed that when the above two were combined, however, their colonization was significantly greater ($P < .05$) than the colonization of dowel for a 20 day period. The values for Float B were generally higher than those for Float A, primarily due to *H. orris*, although they still did not approach the values of the natural snags. Compare, for example, 20-day values from 14 July to 3 August or 50-day values. Also, colonization rates declined in Float B as they did in Float A later in the summer. Again, *Chimarra* sp. appeared to increase over time.

For the deep-water samplers, the hydropsychids colonized heavily after three weeks, yet *Ceraclea* sp. was the only other caddisfly that appeared in any numbers (Table 7). After six weeks, *H. orris* densities declined somewhat, and *M. carolina* and *Ceraclea* sp. showed no consistent change on both samplers. *Chimarra* sp. showed a large increase from

Table 6. Colonization of different wood types on surface sampler Float B for 20, 30, and 50 day intervals. Numbers in parentheses are standard errors.

		Sampling Interval (Days)					
		20 day (14 July - 3 Aug.)		20 day (3 Aug. - 29 Aug.)		20 day (14 July - 3 Sept.)	
Species	Wood Type	Density (no./m^2)	Standing Stock (g/m^2)	Density (no./m^2)	Standing Stock (g/m^2)	Density (no/m^2)	Standing Stock (g/m^2)
Hydropsyche orris	Fresh	1618(243)	1.14(.399)	75(23.0)	.02(.009)*	198(70.4)	.13(.064)
	Old	832(315)	.28(.135)	53(20.2)	.05(.039)*	230(86.5)	.09(.042)
	Dowel	101(45.6)	.04(.014)	28(17.0)	.01(.006)**		
Macronema carolina	Fresh	62(25.8)	.01(.005)	20(12.9)	.00(.001)	159(219)	.03(.010)
	Old	97(67.3)	.02(.011)	0	.00	513(46.2)	.08(.033)
	Dowel	18(18.3)	.00(.000)	14(14.0)	.01(.630)**		
Chimarra sp.	Fresh	0	0	13(12.6)	0*	84(112)	.01(.011)
	Old	0	0	0	0*	181(55.6)	.01(.005)
	Dowel	0	0	14(14.0)	0**		

* Comparable 20 day colonization during same period on Float A showed no colonization.

** 30 day, through 3 September.

Table 7. Colonization of four deep-water samplers for three and six week intervals. (Numbers in parentheses are standard errors).

24 July - 14 Aug.

	Density (No./m^2)	Standing Stock (g/m^2)	Density (No./m^2)	Standing Stock (g/m^2)
	Sampler #1		Sampler #2	
Ceraclea sp.	23.8 (23.8)	.009 (.009)	167.3 (77.1)	.097 (.044)
Chimarra sp.	26.8 (26.8)	.006 (.006)	7.0 (7.1)	.000
Hydropsyche orris	4774.2 (395.3)	3.701 (.203)	5332.4 (720.4)	3.925 (.739)
Macronema carolina	59.9 (45.5)	.048 (.042)	200.7 (182.4)	.162 (.160)

24 July - 3 Sept.

	Density (No./m^2)	Standing Stock (g/m^2)	Density (No./m^2)	Standing Stock (g/m^2)
	Sampler #3		Sampler #4	
Ceraclea sp.	64.9 (25.2)	.042 (.024)	62.1 (29.3)	.027 (.014)
Chimarra sp.	220.3 (133.5)	.001 (.001)	347.9 (153.7)	.007 (.003)
Cyrnellus sp.	449.1 (191.9)	.109 (.043)	177.7 (141.2)	.052 (.050)
Hydropsyche orris	1683.3 (417.3)	1.244 (.305)	3557.3 (630.9)	2.378 (.605)
Macronema carolina	146.2 (69.3)	.060 (.039)	253.4 (21.8)	.128 (.036)
Neureclipsis sp.	24.8 (17.9)	.002 (.001)	7.7 (7.7)	.001 (.001)

three to six weeks and *Cyrnellus* sp. appeared in high densities at the later date. Thus, while total standing stock actually decreased from three to six weeks (due to *H. orris*), diversity increased. By September, densities and standing stocks on the deep-water samplers had come close to those of the natural snags. The total trichopteran density at the lower site on 30 August was 4816 animals/m^2, versus 2605 animals/m^2 on Sampler 3 and 4406 on Sampler 4. This suggests that a considerable time (> month) is needed for communities colonizing an introduced substrate to reach an equilibrium of species.

CHAPTER V

DISCUSSION

Species Distribution and Trophic Relationships

The results presented in this study show the importance of the Trichoptera, the filter-feeding hydropsychids in particular, to this riverine system. Others (Roback 1962, Gordon and Wallace 1975) have noted the dominant role of this family in such systems. In addition, the species distribution found here corresponds well with that found by Gordon and Wallace (1975) on the Savannah River (Georgia - South Carolina): *Hydropsyche orris* and *Macronema carolina* as inhabitants of large Coastal Plain rivers, *Cheumatopsyche* sp. and *Hydropsyche incommoda* being present in large lower Piedmont-Coastal Plain rivers. Gordon and Wallace also noted that the larvae of *H. orris*, *M. carolina*, *H. incommoda* and *Cheumatopsyche* primarily inhabited fallen branches and tree limbs.

It has been suggested (Gordon and Wallace 1975) that the distribution of filter-feeders may be determined by their feeding habits rather than by water quality parameters. In the present study, all the major species were filter-feeders, supported mainly by allochthonous input. *H. orris*, with a net mesh size of 109 x 80 μ for the last instar larvae, has the smallest mesh size of any *Hydropsyche* sp. found to date (Wallace and Sherberger 1974). The net mesh sizes of the other hydropsychids have been reported as 5 x 40 μ for *M. carolina* (Wallace and Sherberger

1974), 150 x 260 μ for H. incommoda (Wallace 1975b), and 77 x 11 μ for Cheumatopsyche, probably C. analis Banks (Wallace 1975b). Attempts to explain differences in hydropsychid species composition at the two sites by particle size preferences incur difficulties because there is some species overlap and other species occur at both sites. For example, Chimarra sp. is common at both sites, and C. socia (probably the species in the Satilla) is one of the finest particle feeders of any trichopteran with a net mesh size of 0.8 x 3-9 μ (Wallace and Malas 1976). It is possible that these animals occupy a micro-habitat that suits their particular needs, i.e., positioning themselves in areas of reduced current where larger particles cannot be transported (Williams and Hynes 1973). It is also possible that similar species such as H. orris and H. incommoda are restricted in their ranges by interference competition.

Other filter-feeders found in the Satilla, Neureclipsis sp. and Cyrnellus sp., construct a trumpet net, which has a funnel-shaped opening (Ross 1944). Neureclipsis bimaculata appears to have randomly arranged silk strands of extremely variable size (Brickenstein 1955). The remaining caddisflies are members of the family Leptoceridae, and are usually thought to be grazers or predators (Ross 1944, Cummins 1974).

Filter-feeding species comprised 99.6% of the total Trichoptera production at the lower site, and 99.9% at the upper site. Since the food of filter-feeders is usually of allochthonous origin, it indicates that autochthonous production is low in the Satilla. This is probably due to the dark color and shifting sand bottom.

Life Histories, Densities and Production

While many studies of the Trichoptera have indicated univoltine life cycles (e.g. Resh 1976), a few cases of bivoltinism in hydropsychids have been reported (Fremling 1960, Rhame and Stewart 1976). All hydropsychids studied to date appear to have five instars. That only four instars were found in *Cheumatopsyche* sp. in the present study may have been due to an inability to collect the earliest instar. Oswood (1976) found four species of hydropsychids in a Montana Lake outlet; three were univoltine and one was apparently bivoltine. The larvae of these similar species tended to overwinter in different instars. Fremling (1960), on a study of the upper Mississippi River, found three species, including *Hydropsyche orris*, and *Cheumatopsyche campyla*, to be bivoltine. The larvae overwintered in the last instar and emerged in late spring. This was followed by a shorter summer generation. Rhame and Stewart (1976) found similar life cycles for *H. simulans*, *C. campyla* and *C. lasia* in the Brazos River, Texas. In the present study, *H. orris* and *H. incommoda* had a similar long winter generation and a short summer generation. *Macronema carolina* life history information indicated the presence of only one generation per year.

Although the combined trichopteran values in the present study are often greater than 5000 animals/m^2 and 5 g/m^2, with maximum values of 46,110 animals/m^2 and 17.3 g/m^2, high figures have been reported elsewhere. Oswood (1976) found benthic hydropsychid densities to have a maximum of over 25,000 animals/m^2, and Rhame and Stewart (1976) presented maximum hydropsychid values of greater than 10,000 animals and

5 g/m^2 (dry weight) for benthic organisms. Their mean standing stock for the year was 2.6 g/m^2. Nord and Schmulback (1973) reported trichopteran densities in the Missouri River of 7290 animals/m^2 on Hester-Dendy samplers after 32 days, with nearly 80% of that number being *Hydropsyche*. Nilsen and Larimore (1973), in the Kaskaskia River, Illinois, found an average of 1900 caddisflies/m^2 on three naturally occurring wood substrates. The above figures reflect the considerable importance of trichopterans, and particularly hydropsychids, in riverine systems.

For the Trichoptera only, the lower and upper site in-channel snag habitat had an annual dry weight production of about 28 and 11 g/m^2 of habitat, respectively. The densities, standing stocks, and production reflect both river conditions and life cycle stages. Sampling when the water was rising or had just risen, such as 1 February, 25 April, 19 July and 1 August (Fig. 2), yielded far fewer animals than expected because the recently inundated habitat had not yet been fully colonized by the snag organisms. From mid-July to mid-August, the Satilla was unusually high. When those few poor sampling dates cited above were eliminated, the annual production of *H. orris* increased from 22.1 to 27.3 g/m^2. Proportionately higher values could be expected for the other species.

The total production was based mainly on those species for which good life history information was obtained. Those species for which little life history information was gained, either in the field or in the literature, contributed little to the total production.

Mann (1975) has reviewed a number of production values reported for rivers. He suggests that annual secondary production will often be a few hundred Kcal/m^2 (or about 50-100 g/m^2 dry weight). Nelson and Scott (1962) on the Oconee River in the Georgia Piedmont, gave values of 57 g/m^2 dry weight for all invertebrates, of which about 30 g/m^2 was contributed by filter-feeders. The values for Trichoptera in the Satilla are close to the values for filter-feeders in the Oconee, and are not much below the range of values for total secondary production suggested by Mann (1975).

Very little information is specifically available on Trichoptera production in rivers at present, but the high densities and standing stocks reported by Rhame and Stewart (1976) and Oswood (1976) indicated that Trichoptera production in those studies could be comparable to that in the Satilla. Of the few estimates of Trichoptera production made in smaller streams, most are much smaller than values found in the Satilla River (Pearson and Kramer 1972, Otto 1975, Resh 1977, Cushman, Hildebrand and Elwood 1975). For example, Cushman et al (1975) found annual production of Diplectrona modesta (Hydropsychidae) to be only about 1 g/m^2 wet weight in a small Tennessee stream. The highest value appeared to be 4.3 g/m^2 dry weight for Oligophlebodes sigma in a small Utah stream (Pearson and Kramer 1972). In general, it appears that secondary production in streams in frequently less than in rivers (Mann 1975).

Substrate Colonization

Colonization of artificial substrates has commonly been used to determine the community structure of aquatic habitats. In the present study it helps to explain the effects a changing habitat has on the snag organisms. While there are many problems associated with substrate sampling (see Hynes 1970 and Cummins 1975), most methods tend to effectively collect the more abundant organisms. In a review of the methods used, it was found that multiplate and basket samplers were the most popular (Mason, Wever, Lewis and Julian 1973).

Usage of indigenous wood for the artificial samplers avoided some of the problems common to quantitative macrofaunal sampling. Like multiplate samplers and the contents of basket samplers and trays, the substrate surface areas could be readily calculated. However, by taking sections of branches near the water for use in all the substrate samplers (except the dowels on Float B), I was assured of providing the organisms with their natural habitat. Colonization might be expected to occur here much in the same manner as it would on recently inundated natural snag habitat.

Recolonization of submerged substrates is believed to come mainly from the drift (Williams and Hynes 1976). Fremling (1960) thought that first-instar larvae of *Hydropsyche orris* were free-swimming, so one might expect them to be a good source of colonization. This also might explain why first instar larvae were not as abundant on the natural snags as expected (Tables 3 and 4). Wallace (1975a) found that later instar larvae of the same species use a silk string attachment to reduce both frequency and distance of drift. Yet, after three weeks their densities were high on the deep-water samplers used in the present study. Although the colonization of the surface samplers never reached natural abundance levels, their pattern of colonization suggested *H. orris* can fully colonize new substrates even more rapidly.

The deep-water samplers were set out to determine if colonization occurred as readily near the bottom as it does near the surface where the natural snags were collected. Since colonization on these samplers approached the densities and standing stocks of the natural snags after three weeks, it appears that abundance and production is similar on snags at all depths. Fremling (1960) found that the size distribution and species composition of larvae on a buoy chain in the Mississippi River were similar from surface to the bottom. However, Nilson and Larimore (1973), working in the Kaskaskia River, Illinois, noted greater densities of caddisflies at an intermediate depth of 54 cm than near the surface or sandy bottom.

Because the natural snags were collected near the surface and were usually heavily colonized, colonization of the surface samplers was obviously lower than expected. This low colonization may have been due to (1) their tendency to collect surface debris, (2) current interference by upstream branches, (3) disturbance by curious fishermen, or (4) algal growth in the branches, probably due to a constant level of submergence. Regardless of the degree of colonization, results from Float A indicated maximum *Hydropsyche* densities are reached in a very short time. The deep snag results suggested more time (six weeks) was needed for greatest diversity. Nord (1971) noted that at least two weeks were needed for organisms colonizing substrates in the Missouri River to be representative of the natural community. Results from Float B indicated, as has been shown elsewhere (Dickson and Cairns, 1972), that lack of substrate diversity (such as dowels in the present study) results in less colonization.

The results from the substrate samplers suggest that many of the natural snag samples probably did not sample all species equally well since it appears to take several weeks for the entire trichopteran community to stabilize. For this reason, the natural samples probably overemphasized the hydropsychids, but this bias should not greatly affect the total production estimates.

CHAPTER VI

CONCLUSIONS

Most studies on invertebrate production of running waters have concentrated on the benthos. However, the Satilla River, located in the coastal plain of Georgia, has a shifting sand bottom that precludes the development of an extensive macrofauna. In spite of this and the fact that it is acidic and darkly colored, the Satilla is able to assimilate energy in the form of secondary production by means of heavy colonization of submerged snags along the river's shoreline. One of the most important groups present on the snags was the Trichoptera.

This study represents the first attempt to estimate production of an entire trichopteran group on a species by species basis. The production estimates for the Trichoptera in the Satilla (11-28 g/m^2 dry weight) were the highest reported to date. Over 99% of secondary production by the Trichoptera was attributed to the filter-feeders.

Results from natural snag samples and introduced substrate samplers indicated that colonization is intense and occurs rapidly. This suggests that secondary production in the Satilla may be limited by suitable habitat. Densities and production of caddisflies also appeared to depend upon substrate submergence time, current speed and time of year.

These results have important management implications. Snags are a predominant feature along the banks of the Satilla. The organisms inhabiting the snags are important as food for predators such as fish, and may be largely responsible for the productive fish fauna of the river.

The removal of snag substrates through desnagging operations or from channelization would probably cause a great decline in the sports fishery presently enjoyed on the river.

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